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Caligoid Copepods Parasitic on *Isurus oxyrinchus* With an Example of Habitat Shift

By Roger F. Cressey
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Several recent collections of parasitic copepods from 17 specimens of the mako shark, *Isurus oxyrinchus*, have made possible redescriptions of certain species of these parasites commonly found on this shark. These, plus 15 collections from the Indian and Atlantic Oceans previously reported (Cressey, 1967a and 1967b), form the basis of this paper.

Ten species of caligoid copepods are reported herein. Both sexes of *Nemesis lamna* Risso and the males of *Dinemoura producta* (Müller) and *D. latifolia* (Steenstrup and Lütken) are redescribed. The last copepodid instar and three chalimus stages of *Phyllothereus cornutus* (Milne-Edwards) males are described for the first time. The remaining species have been redescribed recently by various workers (Shiino, 1955; Lewis, 1966; and Cressey, 1967a), and no further redescription of these species is considered necessary.

All drawings have been made with the aid of a camera lucida. All specimens are preserved in 70 percent alcohol and deposited in the U.S. National Museum.

Station data for the R. V. *Anton Bruun* stations cited in this paper are as follows:

station number	date	latitude	longitude
552	2/17/66	33°02′S	77°02′W
553	2/19/66	33°24′S	79°00′W
554	2/20/66	32°58′S	81°31′W
558	2/24/66	30°28′S	89°31′W
564	3/ 7/66	20°37′S	83°20′W
567	3/10/66	12°50′S	83°31′W
568	3/11/66	10°33′S	83°38′W
569	3/12/66	08°49′S	83°33′W
571	3/14/66	08°47′S	81°20′W
572	3/15/66	10°28′S	79°36′W

I acknowledge the support of the National Science Foundation-Southeastern Pacific Biological Oceanographic Program for supporting a portion of the field work and the Smithsonian Research Foundation for supporting a portion of the laboratory work. I thank Mr. John Casey, Sandy Hook Marine Laboratory, for a collection of shark copepods, a portion of which have been used in this study.

Pandarus satyrus Dana

Pandarus satyrus.—Lewis, 1966, p. 74.
Pandarus cranchii.—Hewitt, 1967, p. 249 [not *P. cranchii* Leach].
For earlier synonymy, see Cressey, 1967a, p. 6.

MATERIAL.—Four collections from off the west coast of South America, R. V. *Anton Bruun*, Cruise 14, Stations 553, 564, 569, and 571; two collections from the Indian Ocean previously reported (Cressey, 1966b); one collection from off New Jersey.

This copepod has been well figured and described in recent literature, and no further description is included here except as related to the remarks below.

REMARKS.—In the seven collections reported above, this copepod was found in the mouth or on the gill arches of the host. *Pandarus satyrus* is a common parasite on the body surface of *Prionace glauca*. In all cases the egg-bearing females of *P. satyrus* from *I. oxyrinchus* were pigmented less noticeably than individuals of the same species when they occur on the body surface of blue sharks. The record of *P. cranchii* cited by Hewitt from the "jaws and skin" of *I. oxyrinchus* appears to be *P. satyrus* according to his figures (figs. 141–147).

Pandarus smithii Rathbun

Pandarus smithii.—Lewis, 1966, p. 91.
For earlier synonymy, see Cressey, 1967a, p. 11.

MATERIAL.—Three collections from the North Atlantic (two off New Jersey, one at 35°N–70°W): one collection from the Indian Ocean, R. V. *Anton Bruun*, Cruise 5, Station 282.

As in *P. satyrus*, this copepod has been redescribed recently (Cressey 1967a), and no further description will be given here.

REMARKS.—The copepods of this species from the Atlantic were found in the mouth of the host. The single female representing the Indian Ocean collection from this host was on the body surface. Like *P. satyrus*, this copepod is a common parasite on the body surface of sharks, primarily carcharinids. Also, as in *P. satyrus*, those specimens from inside the buccal area of the host are not pigmented as heavily as individuals of the same species occurring on the body surface of other sharks.

Pandarus katoi, Cressey

Pandarus katoi Cressey, 1967a, p. 17.

MATERIAL.—Four collections from off the west coast of South America, R. V. *Anton Bruun*, Cruise 14, Stations 567, 568, 569, and 571.

REMARKS.—*Pandarus katoi* has been reported previously from the body surface of carcharinid sharks in the eastern Pacific (Cressey, 1967a). The collections recorded above from *I. oxyrinchus* were removed from the mouths and gill arches of the hosts. The specimens in collections of this species from the body surface of other sharks are not pigmented as heavily as most other species of the genus *Pandarus;* nevertheless, the *P. katoi* from the mouths of makos are pigmented still less than those on the body surface of other sharks, consistant with the situation with *P. satyrus* and *P. smithii* reported above. The change in habitat for these three species is discussed at the end of this paper.

Gangliopus pyriformis Gerstaecker

For earlier synonymy, see Cressey, 1967a, p. 28.

MATERIAL.—One collection off the west coast of South America, R. V. *Anton Bruun*, Cruise 14, Station 552 (1 ♀ specimen only).

REMARKS.—The single specimen from the 32 sharks examined indicates a low incidence of this parasite. This copepod is more common on *Prionace glauca* and, since these two sharks often are found in the same waters, this may be a reflection of that association.

Phyllothereus cornutus (Milne-Edwards)

FIGURES 1–26

Phyllothereus cornutus.—Lewis, 1966, p. 96.—Hewitt, 1967, p. 233.
For earlier synonymy, see Cressey, 1967a, p. 25.

MATERIAL.—Four collections off the west coast of South America, R. V. *Anton Bruun*, Cruise 14, Stations 553 (two collections), 554, and 572.

Many immature stages including the last copepodid stage were collected from the sharks off South America. When some of these copepodids were cleared in KOH and lactic acid, the first chalimus stage could be seen within. By carefully splitting open the copepodid, I teased out the developing chalimus. These chalimus stages were identical to first chalimus stages collected free in the gill chamber of the shark. Two successive chalimus stages also were found. These immature stages are described below. For a description of the adults of this species, see Cressey (1967a).

LAST COPEPODID.—Body form as in figure 1. Total length 6.77 mm (6.23–7.43) based on an average of 240 specimens, greatest width 4.07 mm (3.78–4.38) based on an average of 20 specimens (all measured specimens taken from a single shark at R. V. *Anton Bruun* Station 554).

Dorsal surface unornamented. Two "eye spots" with more heavily pigmented area surrounding and between them in anterior third of cephalon. Posterior corners of first free thoracic segment produced, extending nearly to end of second free thoracic segment. Genital segment slightly longer than wide (1.3 x 1.1 mm in one specimen). Abdomen 1-segmented, somewhat triangular, wider than long (.3 x .4 mm in one specimen). Caudal ramus (fig. 2) 536μ wide, 590μ long at outer edge, 295μ long at inner edge (based on one specimen); armed with six plumose setae, four long terminal and two short subterminal. Adhesion pad present on ventral surface immediately posterior to first antenna.

First antenna (fig. 3) 2-segmented: basal segment with several short plumose spines, proximal two more heavily spinose; terminal segment with seven setae, posterior four plumose. Second antenna (fig. 4) with terminal segment in form of a claw, tip of claw twisted. Mouth tube and mandible of usual caligoid form, mandible with 10 teeth. First maxilla (fig. 5) a small lobe with three short setae and posterior projection bearing process with rugose tip. Second maxilla (fig. 6) with two terminal claws and subterminal hirsute process, claws ornamented as in figure 7. Maxilliped (fig. 8) stout, bearing bladelike claw opposed by striated area on basal segment.

Legs 1–4 (figs. 9–12) biramose. Rami of legs 1–3 2-segmented. Exopod of leg 4 1-segmented, endopod 2-segmented (see spine and seta formula below). Leg 5 (fig. 13) a knob bearing two setae, one naked and one plumose, on lateral margin of genital segment. Leg 6 absent.

Color in life: dark mahogany brown.

CHALIMUS I, MALE.—Body form as in figure 14. Total length 6.6 mm, greatest width 3.1 mm (all measurements based on a single specimen taken from the same shark as copepodids).

Dorsal surface unornamented. Eye spots less obvious than in copepodid. Outer posterior corners of first free thoracic segment produced, extending nearly to end of second free thoracic segment. Genital segment as wide as long (1.4 x 1.4 mm), posterior corners produced to form short rounded lobes. Abdomen 2-segmented; each segment about same length but second segment somewhat wider than first and triangular (widest posteriorly). Caudal rami triangular; with four long terminal and two short subterminal plumose setae. Adhesion pad on ventral surface posterior to base of first antenna.

First antenna (fig. 15) 2-segmented, similar to copepodid except that segments longer, bearing more setae. First maxilla (fig. 16) similar to copepodid except rugose process of copepodid is short pointed process in chalimus I. Second maxilla of chalimus I and all subsequent stages with plumose processes at base of two terminal spines (see Cressey, 1967a, fig. 129). Maxilliped (fig. 17) with pointed claw, seta on inner margin of claw. Legs 1–4 biramose. All rami 2-segmented. Leg 1 exopod with four spines equal in length on outer terminal margin of second segment, endopod of first segment with adhesion pad on inner distal corner. Leg 2 exopod with four outer spines, distalmost about twice length of proximalmost spine. Leg 3 exopod with four outer spines, proximalmost very small; other three becoming progressively longer, distalmost twice length of next longest. Leg 4 exopod with four spines, lengths as in leg 3. Leg 5 consisting of spine and two plumose setae at notch at posterior three-fourths of genital segment. Leg 6 a single spine near junction of abdomen and genital segment.

Color in life: cream.

CHALIMUS II, MALE.—Body form as in figure 18. Total length 8.6 mm, greatest width 4.6 mm (all measurements based on single specimen). Clear fringe around cephalon and outer corners of first free segment (not seen in previous stage). Principle changes in body form from previous stage are proportionately wider cephalon, elongation of genital segment, and more prominent caudal rami. Adhesion pads present ventrally on cephalon, one posterior to base of first antenna and a small one on basal segment of second antenna.

First antenna (fig. 19) with both segments longer and with increased ornamentation over previous stage. Second antenna (fig. 20) with well-developed claw; bearing two short setae, one at base of claw and one median. Maxilliped (fig. 21) with well-developed claw. Other head appendages as in previous stage.

Legs 1–4 biramose (see pls. 1–4). Spine and seta formula for legs 1–4 of last three immature stages and adult male are as follows (Roman numerals refer to spines, arabic to setae):

leg	seg.	copepodid exo.	copepodid end.	chalimus I exo.	chalimus I end.	chalimus II exo.	chalimus II end.	chalimus III exo.	chalimus III end.
1	1	I:0	0:0	I:0	0:0	I:0	0:0	I:0	0:0
	2	IV:3	3	IV:3	3	IV:3	3	IV:3	3
2	1	I:1	0:1	I:1	0:1	I:1	0:1	I:1	0:1
	2	IV:5	7	IV:5	8	IV:6	8	IV:6	8
3	1	I:0	0:1	I:1	0:1	I:1	0:1	I:1	0:1
	2	III:4	4	IV:5	5	IV:5	6	IV:5	6
4	1	IV:3	0:1	I:0	0:1	I:1	0:1	I:1	0:1
	2		3	IV:5	4	IV:5	5	IV:5	5

Leg 5 (fig. 22) consists of single stout spine and three short plumose setae at notch in margin of genital segment (an increase of one seta over previous stage). Leg 6 a short spinelike process with plumose seta near junction of abdomen and genital segment.

The lengths in mm of each of the free body segments for the last five developmental stages of the male are as follows (specimens measured along mid-dorsal, anterior-posterior axis):

	copepodid	chalimus I	chalimus II	chalimus III	adult
cephalon	2.4	2.6	3.2	3.6	5.3
first free thoracic segment	.9	.6	.7	.9	.9
second free thoracic segment	.7	.6	.8	.8	1.2
third free thoracic segment	.9	.8	.9	.9	1.3
genital segment	1.3	1.4	1.7	2.3	3.8
abdomen	.3	.3	.5	1.0	1.4
caudal ramus	.1	.6	.8	.9	2.0
total body length	6.6	6.6	8.6	10.4	15.9

CHALIMUS III, MALE.—Body form as in figure 23. Total length 10.4 mm, greatest width 4.9 mm (measurements based on single specimen). This form is ornamented in all respects like chalimus II. There is a general increase in size and further elongation of genital segment. Cephalic appendages show elongation of terminal segments when compared with previous stage (claw of second antenna, maxilliped and terminal segment of first antenna are proportionally longer). Other than subtle changes in proportions, appendages are the same as in chalimus II. For comparison of legs 1–4, see plates 1–4.

ADULT MALE.—Total length 15.9 mm, greatest width 7.2 mm (measurements based on one specimen). The appendages of the adult do not differ significantly from the previous stage except for subtle changes in lengths of terminal segments of cephalic appendages, the adult appendage is somewhat longer in proportion (compare adult first maxilla, fig. 24 with fig. 16). The maxilliped of the adult male (fig. 25) bears two striated pads opposing the claw instead of just one as in previous stages.

Changes in ornamentation and proportionate lengths of the segments of the first antenna of all stages of the male are as follows:

	segment 1			segment 2		
	length	percent total length	no. spines and setae	length	percent total length	no. spines and setae
copepodid	266μ	66	14	136μ	34	5
chalimus I	342μ	68	23	165μ	32	12
chalimus II	413μ	64	27	236μ	36	14
chalimus III	472μ	61	27	307μ	39	14
adult	531μ	58	27	378μ	42	14

ADULT, FEMALE.—Body form as in figure 27. For a complete description of the female of this species, see Cressey (1967a).

REMARKS.—The description of the copepodid instar of this species is the first to be linked conclusively to a known species of pandarid copepod. Similar forms have been described as the males of the genus *Nesippus* (Dana, 1852; Steenstrup and Lütken, 1861; Beneden, 1892; Gnanamuthu, 1949; and Hewitt, 1967). This description substantiates my previous remarks regarding these *Nesippus* males (1967a, p. 59). Since no forms intermediate between chalimus III and the adult male were found, it is assumed that there are only three chalimus stages. A few immature females were collected but not enough to determine their stage of development. Description of these forms has been deferred until more material can be collected.

The copepodids were found either on the body surface of the host or within the gill chamber, usually just inside the gill slit. The chalimus stages and adults all were found within the gill chamber but not usually on the filaments themselves. Most often these forms were found near the tips of the filaments, firmly attached to the epidermis. The females often cause the tissue to swell, almost covering the cephalon. Males were not observed to produce this host reaction.

This parasite is not restricted to *Isurus* but also is found commonly on other lamnid sharks and *Prionace glauca*.

Dinemoura latifolia (Steenstrup and Lütken)

FIGURES 26–27

Dinematura latifolia.—Lewis, 1966, p. 102.—Hewitt, 1967, p. 195.
For earlier synonymy, see Cressey, 1967a, p. 42.

MATERIAL.—Three collections in the western North Atlantic (two previously reported by Cressey, 1967a); one collection from the Caribbean Sea, 13°38′N, 75°50′W; five collections from the Indian Ocean, previously reported by Cressey (1967b); eight collections from off the western coast of South America, R. V. *Anton Bruun*, Stations 553, 554, 564, and 567); one collection from the central Pacific, vicinity of Christmas Island.

REMARKS.—Both sexes of this copepod have been described, most recently by Lewis (1966). In my pandarid revision (1967a), I noted the lack of information regarding the male of this species. Lewis provides a good description of this sex in his 1966 paper. My material conforms to his description in every way except in regard to the first antenna (antennule in Lewis). According to Lewis, the first segment bears 14 setules and the second segment, five setae. In my material I have found each segment with more setae than described by Lewis (25 on the first segment, 12 on the second). A figure of the male (fig. 26) and its first antenna (fig. 27) is provided to supplement the description by Lewis.

This copepod is a common parasite on the body surface of mako sharks. Large clusters of females often occur in the posterior half of the body and usually on the ventral surface. Males generally are fewer in number and are scattered over the body surface.

Dinemoura producta (Müller)

FIGURES 28–42

Dinemoura producta.—Hewitt, 1967, p. 204.
For earlier synonymy, see Cressey, 1967a.

MATERIAL.—A single collection previously reported from the North Atlantic (Cressey, 1967a); three collections from off Scripps Pier, La Jolla, Calif.; 12 collections off Chile and Peru, R. V. *Anton Bruun*, Stations 552, 553, 554, 567, 568, 569, 571, and 572.

FEMALE.—A good description of the female of this species was given by Shiino (1957). Additions to his description were provided by Cressey (1967). Further description of the female will not be included herein.

MALE.—The male of this species was described by Wilson (1923) but a redescription of this sex is needed and is provided below.

Body form as in figure 28. Total length 8.25 mm, greatest width 3.6 mm (measurements based on a single specimen from Station 567). Lengths in mm of each of the body segments measured along the mid-dorsal line are as follows:

cephalon	2.55
first free thoracic segment	.37
second " " "	.60
third " " "	.75
genital segment	2.18
abdomen (2 segments)	.90
caudal ramus	.90

No dorsal plates present. Abdomen 2-segmented, second segment about twice as long as first. Genital segment (fig. 29) nearly twice as

long as wide (2.18 x 1.30 mm). Caudal rami (fig. 30) conspicuous, longer than wide (.90 x .52 mm); armed with four prominent plumose setae and two small subterminal plumose setae, inner margins of rami with row of short hairs.

First antenna (fig. 31) 2-segmented; basal segment with 26 short spines and setae, terminal segment with 12 short naked setae. Second antenna (fig. 32) stout; terminal claw with accessory process near base and two setae, one short and one long; appendage armed with number of adhesive areas as indicated in figure. First maxilla (fig. 33) with 3-segmented terminal ramus, basis bearing group of three short setae. Second maxilla (fig. 34) terminal claw with rows of fine hairs; second segment bearing short stout spine covered with fine spinules, patch of hairs on outer distal corner. Maxilliped (fig. 35) well developed; terminal claw opposed by two adhesion areas on basal segment.

Legs 1–4 biramose. Leg 1 (fig. 36) both rami 2-segmented. Exopod first segment large, bearing spine on outer distal corner; second segment with fringe of digitiform processes along outer edge and bearing three short spines and four setae. Endopod first segment unarmed, distal end produced to form broad lamella overlapping base of terminal segment; terminal segment with three stout setae and patch of hairs on outer edge. Leg 2 (fig. 37) both rami 3-segmented. Exopod first two segments of each with spine and seta on outer and inner distal corners respectively, terminal segment with two lateral spines and six setae. Endopod first segment with seta on inner distal corner, second segment with two setae at inner distal corner, terminal segment with six setae. Leg 3 (fig. 38) both rami 3-segmented. Exopod with same armature as leg 2. Endopod with last two segments modified as in figure 39. Leg 4 (fig. 40) rami 2-segmented. Exopod first segment with spines on outer distal corner, second segment with spine on outer and seta on inner distal corners, terminal segment with two spines and five setae. Endopod with one, two, and three setae on the inner margin of each segment respectively.

Spine and seta formula of legs 1–4 is as follows:

	leg 1		*leg* 2		*leg* 3		*leg* 4	
seg.	*exp.*	*end.*	*exp.*	*end.*	*exp.*	*end.*	*exp.*	*end.*
1	1:0	0:0	I:1	0:1	I:1	0:1	I:0	0:1
2	III:4	3	I:1	0:2	I:1	0:2	I:1	0:2
3			II:6	5	II:6	I:4	II:5	3

Leg 5 (fig. 41) represented by process on ventral surface of genital segment bearing one outer fringed spine and two inner plumose setae (see fig. 29); a fourth plumose seta internal to process. Leg 6 (fig. 42) a process near posterior corner of genital segment bearing one outer naked spine and one short inner plumose seta.

REMARKS.—This copepod normally is found on the fins of the host, most frequently on the trailing edges of the dorsal and pectoral fins.

***Echthrogaleus denticulatus* Smith**

Echthrogaleus pellucidus Shiino, 1963, p. 357.
For earlier synonymy, see Cressey, 1967a, p. 56.

MATERIAL.—One collection from off Scripps Pier, La Jolla, Calif.; one collection from the central Pacific in the vicinity of Christmas Island; six collections off Chile and Peru, R. V. *Anton Bruun*, Stations 553, 554, 568, 569, and 571; and four collections from the Indian Ocean previously reported (Cressey, 1967b).

REMARKS.—No description of either sex of this copepod will be given herein as that of Shiino (1963) and of Cressey (1967a) are adequate. I have placed *E. pelludicus* Shiino in synonomy after re-examining the type of *E. denticulatus* Smith deposited in the USNM. The only differences among all the material I have collected recently, the description of *E. pellucidus* by Shiino, and the type-specimen is that the type is larger. The type-specimen was collected in the North Atlantic, whereas all other material has come from the Indo-Pacific. Cressey (1967a, p. 27) reported a similar situation for another species of parasitic copepod, *Phyllothereus cornutus*, where the specimens collected from the colder waters of the Atlantic were larger than those from the relatively warmer Indian Ocean.

These copepods generally are found on the body surface of the host, frequently in the anterior part near the gill slits. Although there was a high incidence of infestation on mako sharks off Chile and Peru, the number of individuals on any one shark was never more than 20. This same species was collected in the Indian Ocean from thresher sharks, *Alopias vulpinus*, and often occured on that host in clusters of more than 100 individuals.

***Anthosoma crassum* (Abildgaard)**

For earlier synonymy, see Lewis, 1966, p. 66.

MATERIAL.—Four collections from off Scripps Pier, La Jolla, Calif.; four collections from the central Pacific in the vicinity of Christmas Island; one collection from off Sandy Hook, N.J.; two collections from the Indian Ocean, previously reported (Cressey, 1967b); one collection from the North Atlantic taken during a cruise of the M. V. *Delaware*; seven collections from off Chile and Peru, R. V. *Anton Bruun*, Stations 552, 553, 554, 558, 564, 568, and 571.

REMARKS.—This species has been well described by Shiino (1955) and Lewis (1966) and no further description will be given herein. On the mako sharks caught off the western coast of South America, this species was very common and was always found imbedded be-

tween the teeth on either or both the upper and lower jaw. It has been recorded also from other species of lamnid sharks.

Nemesis lamna Risso

FIGURES 43–58

Nemesis lamna Risso, 1826, p. 136.—Roux, 1828, p. 174.—Guérin, 1837, pl. 35.—Krøyer, 1837, p. 199.—Milne-Edwards, 1840, p. 486.—Wilson, 1922, p. 59; 1932, p. 461.—Fage, 1923, p. 282.—Heegaard, 1962, p. 184.—Cressey, 1967b, p. 6.

Nemesis carchariarum Roux, 1828, p. 176.—Krøyer, 1837, p. 199.—Milne-Edwards, 1840, p. 486 [misspelled "*carcherium*"].

Nemesis mediterranea Heller, 1868, p. 220.—Valle, 1880, p. 66.—Richiardi, 1880, p. 151.—Stossich, 1880, p. 262.—Carus, 1885, p. 365.—Brian, 1898, p. 15; 1899, p. 201; 1902, p. 44; 1905, p. 7.—Bassett-Smith, 1899, p. 476.

Nemesis lamna var. *sinuata*.—Valle, 1878, p. 91.

MATERIAL.—Four collections from the Indian Ocean, previously reported (Cressey 1967b); three collections from off Scripps Pier, La Jolla, Calif.; nine collections from off the Coast of Chile and Peru, R. V. *Anton Bruun*, Stations 552, 553, 554, 558, 564, and 572.

FEMALE.—Body form as in figure 43. Total length 6.61 mm (5.85–7.95), greatest width 2.0 mm (1.73–2.40). Widths of cephalon and four free thoracic segments are as follows: cephalon 1.25 mm (1.19–1.50), first free thoracic segment 1.92 mm (1.80–2.33), second free thoracic segment 2.00 mm (1.73–2.40), third free thoracic segment 1.99 mm (1.73–2.40), fourth free thoracic segment 1.74 mm (1.50–2.25). All measurements are based on an average of 10 ovigerous females randomly selected from the collection at Station 552.

Fourth free thoracic segment (bearing leg 5) with many sclerotized papillae on dorsal surface. Genital segment (fig. 44) about as long as wide (.8 x .8 mm) and subdivided ventrally giving the appearance of two segments. Abdomen (see fig. 44) 2-segmented. Each segment with a few papillae on dorsal surface and armed with short hairs and spinules as in figure. Caudal rami short, about twice as long as wide (363μ x 218μ), bearing rows of short spinules on ventral surface.

First antenna (fig. 45) composed of 13 segments. Each segment armed with short setae as in figure. Second antenna (fig. 46) 4-segmented, basal segment with weak triangular process on inner surface, antepenultimate segment with short seta on inner distal corner, penultimate segment unarmed, terminal segment in form of short claw bearing two setae on inner border. Mouth tube and mandible of usual caligoid type, mandible with eight to nine teeth. First maxilla (fig. 47) biramose; each rami with two setae, anteriormost ramus with one short and one long seta. Posterior ramus with two equal long setae. Tip of second maxilla (fig. 48) with short claw, claw covered with short papillae. Patch of spines present near base of claw

and patch of long hairs on outer corner of segment bearing terminal claw. Maxilliped (fig. 49) in form of stout claw. Penultimate segment with triangular process on inner proximal corner. Claw heavily sclerotized and bearing two short setae on inner margin.

Legs 1–4 biramose, each ramus 2-segmented. All legs with conspicuous patches of spinules as indicated in figures. Leg 1 (fig. 50) exopod first segment long and recurved, second segment small bearing three short spines at tip; endopod first segment with outer distal corner produced to form prominent claw, last segment with two weak setae at tip. Second leg (fig. 51) exopod first segment with inner and outer corners produced to form spines, last segment short, bearing six short spines of about equal length; endopod first segment similar to that of exopod, last segment with five spines. Leg 3 (fig. 52) exopod as in leg 2 except last segment bearing seven short spines; endopod first segment as in leg 2, last segment with prominent spinelike process on outer distal corner and one small outer and four small inner spines. Leg 4 (fig. 53) exopod first segment with spine on outer distal corner only, last segment with six small spines; endopod first segment as in legs 2 and 3, last segment with five spines, next to outermost larger than other four. Leg 5 represented by knob bearing three short setae on outer distal corners of genital segment.

MALE.—Body form as in figure 54. Total length 4.7 mm, greatest width 1.6 mm measured across first free thoracic segment (measurements based on single specimen from Station 552).

Cephalic appendages as in female. Leg 1 as in female. Leg 2 (fig. 55) exopod first segment with prominent spine on outer distal corner and small seta on inner margin, second segment with six small setae on terminus and inner margin; endopod first segment with prominent spine on outer distal corner, second segment with three short but somewhat recurved setae. Leg 3 (fig. 56) exopod first segment with outer prominent spine and small seta on inner distal corner, second segment with six setae, fourth from outer considerably longer than other five; endopod first segment with outer distal corner produced to form prominent spine, endopod with two terminal spines and three small setae on inner margin, spine on inner distal corner strong and somewhat recurved. Leg 4 (fig. 57) exopod first segment with prominent spine on outer distal corner, second segment with six setae, inner three longer than outer three; endopod first segment with outer corner produced to form strong spine and inner margin bearing conspicuous seta, second segment with two terminal spines and two inner short setae, spine on inner distal corner strong and slightly recurved as in leg 3. Leg 5 (see fig. 58) a short free segment bearing three setae plus single seta near base of segment. Leg 6 (see fig. 58) on outer distal corner of genital segment consisting of prominent inner spine

and two outer setae. Spermatophores visible within genital segment.

REMARKS.—Wilson (1932) redescribed both sexes of this species and stated that no description had been presented since Heller (1865). He apparently was unaware of the redescription of the female and description of the male by Fage (1923). Although Fage's description is of more value than that of Wilson, both lack certain details and, thus, a redescription of both sexes has been presented herein.

This species is very common on mako sharks and, as in other members of the genus, the adults are found only on the gill filaments of the host. It has been reported from other lamnid sharks as well.

Habital Shift in the Genus *Pandarus*

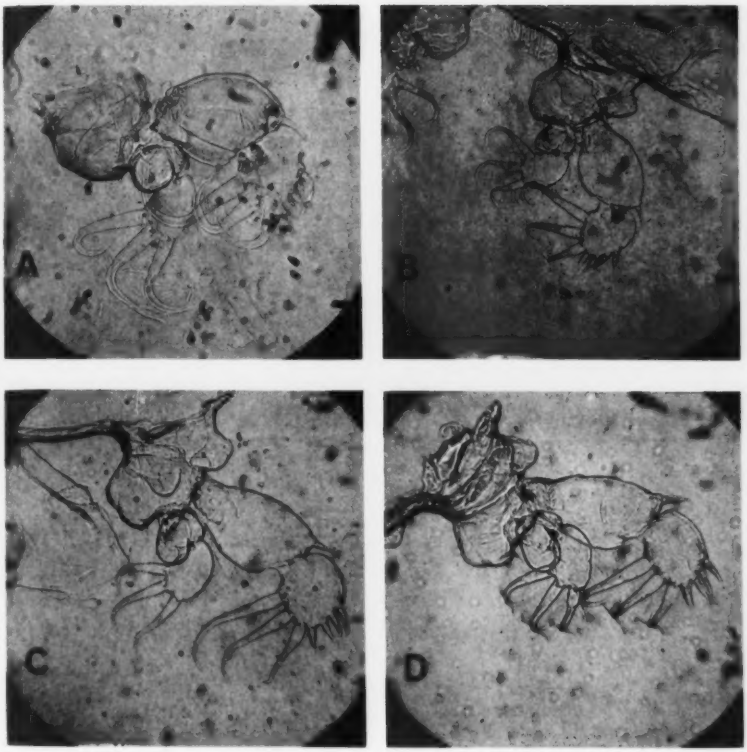
All species of the genus *Pandarus* are found commonly on the body surface of their respective shark hosts. In this paper three species are reported from *Isurus oxyrinchus*. Of the 16 collections of *Pandarus* from this host, only one was taken from the body surface (*P. smithii* in the Indian Ocean). All others were collected from the mouth and/or the gill arches. During the course of my studies with parasitic copepods, it has become evident that there is considerable specificity with regard to the site of infestation on the host. One can predict with a high degree of certainty sites of infestation for any species. Needless to say, any marked deviation from the usual mode of existence presents some interesting problems. Such is the case with the genus *Pandarus* as found usually on *Isurus oxyrinchus*.

While collecting *Pandarus* from the mouths of mako sharks, I suspected that they might represent new species due to the unusual habitat and their noticeable reduction in pigmentation. Subsequent examination, however, showed that they all could be assigned to the known species—*satyrus*, *smithii*, and *katoi*—differing from other members of each species only in the reduced pigmentation. An examination of the collection records showed that in all cases where *Pandarus* was present in the mouth, either *Dinemoura latifolia* and/or *D. producta* were present at the sites where one might expect to find *Pandarus* on other hosts. In the one collection where *Pandarus* occurred on the body surface, *Dinemoura* was not present. Apparently, the presence of *Dinemoura* inhibits *Pandarus* from becoming established in its usual places. The fact that it does become established in a new location is interesting. I suspect that in time, if they continue to be successful in this habitat, they will result in new species of the genus being produced. By the usual criteria of separating the species of the genus, they cannot at present be considered as different species. If, however, their progeny result in forms that will not attach to any other host on the body surface, then they represent something new. A definitive answer to this would come only from experimental evidence and cannot

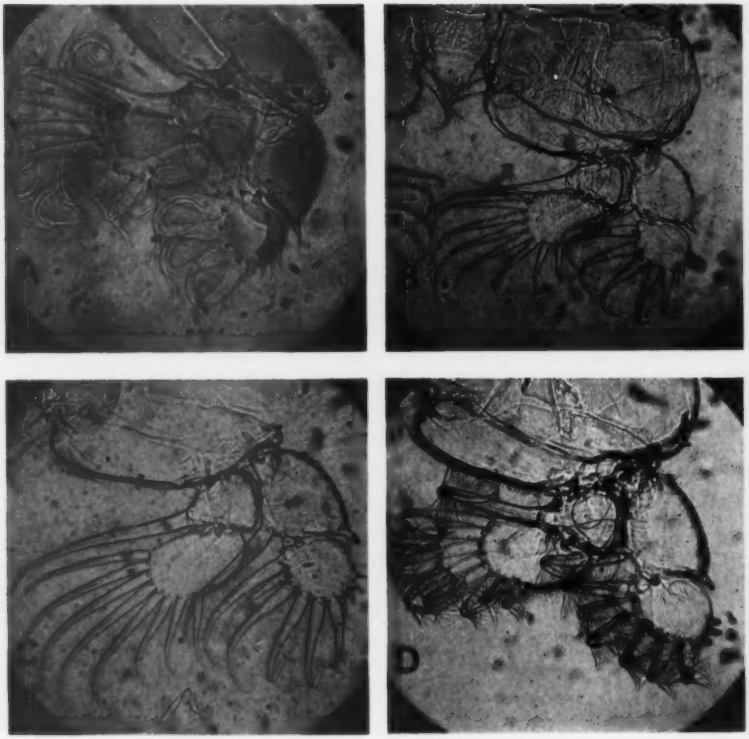
be ascertained at this time. I suspect that this situation represents new species in the early stages of formation.

It is interesting to note that Hewitt (1967) cites two records of *P. cranchii* (which are actually *P. satyrus*) from the "buccal cavity" and "jaws and skin" of *Isurus oxyrinchus* and *Galeorhinus australis*. *Dinemoura latifolia* was collected from both of these sharks.

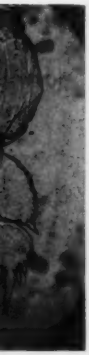
As previously indicated, adult females of the three species in the mouth were pigmented less noticeably than adult females of the same species that occurred on the surface of other hosts. Two possible explanations come to mind. First, the pigmentation may be influenced by the amount of light available to the copepod, those in the mouth receiving less. Second, the pigmentation may be influenced by the amount of pigmentation of the shark at the point of attachment of the parasite. From my own observations of other parasitic copepods, I favor the latter explanation. Often parasitic copepods assume the color of the host tissue to which they are attached, or those parasites with little or no pigment are associated with lighter areas and the pigmented forms are on darker areas. Many questions basic to understanding this departure remain unanswered. Most of these deal with the life history process about which practically nothing is known. No attempt at a definitive explanation is offered here, but rather I have presented the situation in the hope that future investigations will shed more light on this interesting situation.



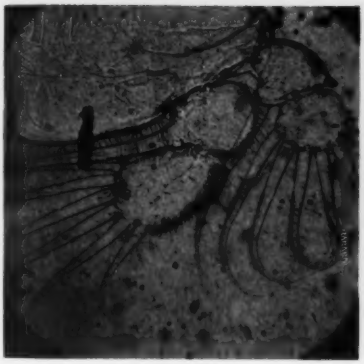
Phyllothereus cornutus, male: *a*, copepodid leg 1; *b*, chalimus I leg 1; *c*, chalimus II leg 1; *d*, chalimus III leg 1.



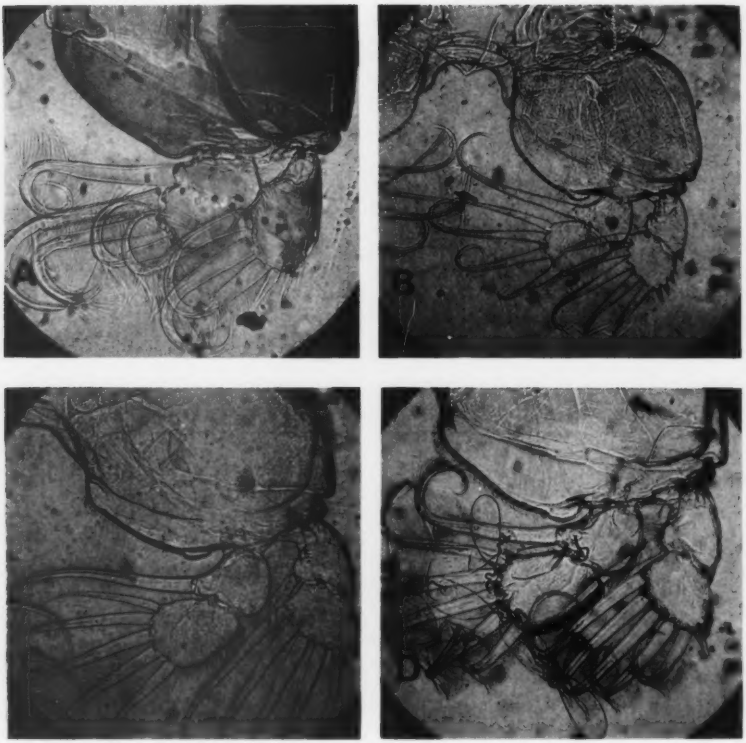
Phyllothereus cornutus, male: *a*, copepodid leg 2; *b*, chalimus I leg 2; *c*, chalimus II leg 2; *d*, chalimus III leg 2.



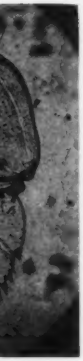
s II leg 2;

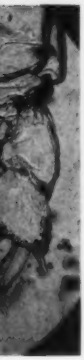


Phyllothereus cornutus, male: *a*, copepodid leg 3; *b*, chalimus I leg 3; *c*, chalimus II leg 3; *d*, chalimus III leg 3.



Phyllothereus cornutus, male: *a*, copepodid leg 4; *b*, chalimus I leg 4; *c*, chalimus II leg 4; *d*, chalimus III leg 4.





s II leg 4;

Literature Cited

BASSETT-SMITH, P. W.

1899. A systematic description of parasitic Copepoda found on fishes, with an enumeration of the known species. Proc. Zool. Soc. London, pt. 2, pp. 438–507.

BENEDEN, P. J. VAN

1892. Le male de certain caligides et un nouveau genre de cette famille. Bull. Belgique, year 62, ser. 6, vol. 23, no. 3, pp. 220–235.

BRIAN, A. G. G.

1898. Catalogo di copepodi parassiti dei pesci della Liguria. Atti. Soc. Lig. Sci. Nat. Geogr., vol. 9, pp. 5–31.

1899. Crostacei parassiti dei pesci dell'Isola d'Elbe, 2: Contribuzione. Atti. Soc. Lig. Sci. Nat. Geogr., vol. 10, pp. 197–207.

1902. Note su alcuni crostacei parassiti dei pesci del Mediterraneo. Atti. Soc. Lig. Sci. Nat. Geogr., vol. 13, pp. 30–45.

1905. Sui copepodi raccolti nei golfo di Napoli da Oronzio G. ed Achille Costa. Ann. Mus. Zool. Univ. Napoli, vol. 1, no. 24, pp. 1–11.

CARUS, J. V.

1885. Prodromus faunae mediterraneae . . . , vol. 1, xi +525 pp.

CRESSEY, R. F.

1967a. Revision of the family Pandaridae (Copepoda: Caligoida). Proc. U. S. Nat. Mus., vol. 121, no. 3570, pp. 1–133.

1967b. Caligoid copepods parasitic on the sharks of the Indian Ocean. Proc. U. S. Nat. Mus., vol. 121, no. 3572, pp. 1–21.

DANA, J. D.

1852–53. Crustacea, pts. 1 and 2. Vol. 13 *in* United States exploring expedition . . . 1838–42 . . . , pt. 1 (1852), viii +685 pp.; pt. 2 (1853), pp. 686–1618.

FAGE, L.

1923. Sur deux copépodes *Dinemoura producta* (Muller) et *Nemesis lamna* (Risso) parasites du pélerin, *Cetorhinus maximus* (Gunner). Bull. Soc. Zool. France, vol. 48, nos. 6 and 7, pp. 280–287.

GNANAMUTHU, C. P.

1949. Two male parasitic copepods from Madras. Ann. Mag. Nat. Hist., ser. 12, vol. 2, pp. 359–367.

GUÉRIN-MÉNEVILLE, F. E.

1837. Crustacés. Vol. 26 *in* Iconographie du regne animal. [1829–1843: plates; 1844: text.]

HEEGAARD, P.

1962. Parasitic Copepoda from Australian waters. Rec. Australian Mus., vol. 25, no. 9, pp. 149–233.

HELLER, C.

1868. Crustaceen. No. 8 *in* vol. 2 *of* Zoologischer Theil *in* Reise der Oesterreichischen Fregatte Novara . . ., 280 pp., 25 pls.

HEWITT, G. C.

1967. Some New Zealand parasitic Copepoda of the family Pandaridae. New Zealand Journ. Mar. Freshw. Res., vol. 1, no. 2, pp. 180–264.

KRØYER, H.
1837–38. Om synltekrebsene, isaer med Hensyn til den Danske Fauna. Naturh. Tidsskr., vol. 1, no. 2, pp. 172–208; no. 3, pp. 252–304; no. 5, pp. 476–506; no. 6, pp. 605–628; (1838), vol. 2, pp. 8–52, 131–157.

LEWIS, A. G.
1966. Copepod crustaceans parasitic on elasmobranch fishes of the Hawaiian Islands. Proc. U. S. Nat. Mus., vol. 118, no. 3524, pp. 57–154.

MILNE-EDWARDS, H.
1840. Histoire naturelle des crustacés, comprenant l'anatimie, la physiologie et la classification de ces animaux, 638 pp., 42 pls.

RICHIARDI, S.
1880. Contribution alla fauna D'Italia: Catalogo sistematico dei corstacei che vivono sul corpo degli animali aquatici. *In* Catalogo degli Espositori, pp. 147–152.

RISSO, A.
1826. Historie naturelle des principales productions de l'Europe méridionale et particulierement de celles des environs de Nice et des Alpes martitimes, vol. 5, 402 pp.

ROUX, P.
1828. Crustacés de la Mediterranee et de son littoral, 176 pp., 45 pls. Paris.

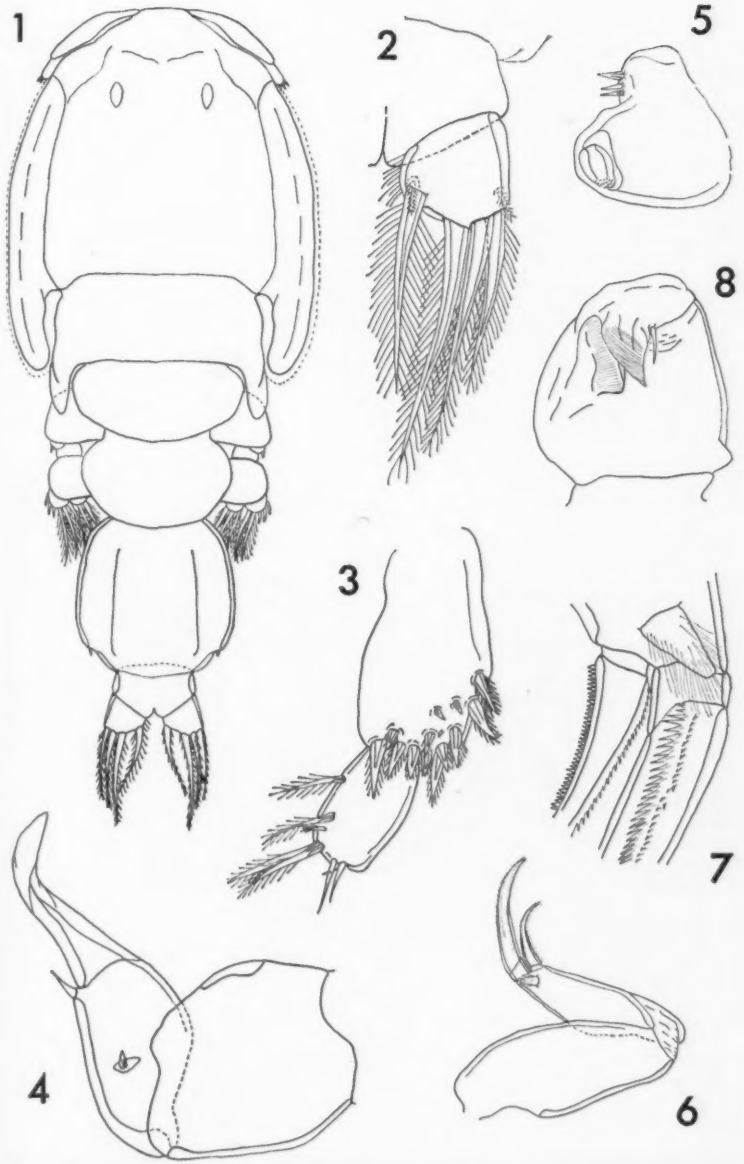
SHIINO, S. M.
1955. Copepods parasitic on Japanese fishes, 8: The Anthosomidae. Rep. Fac. Fish. Pref. Univ. Mie, vol. 2, no. 1, pp. 50–69.
1957. Copepods parasitic on Japanese fishes, 13: Parasitic copepods collected off Kesennuma, Miyagi Prefecture. Rep. Fac. Fish. Pref. Univ. Mie, vol. 2, no. 3, pp. 359–375.

STEENSTRUP, J. J. S., and LÜTKEN, C. F.
1861. Bidrag til Kundskab om det aabne Havs Snyltekrebs og Lernaeer semt om nogle andre nye eller hidtil kun ufuldstaen digt kjendte parasitiske Copepoder, vol. 5, pp. 341–342.

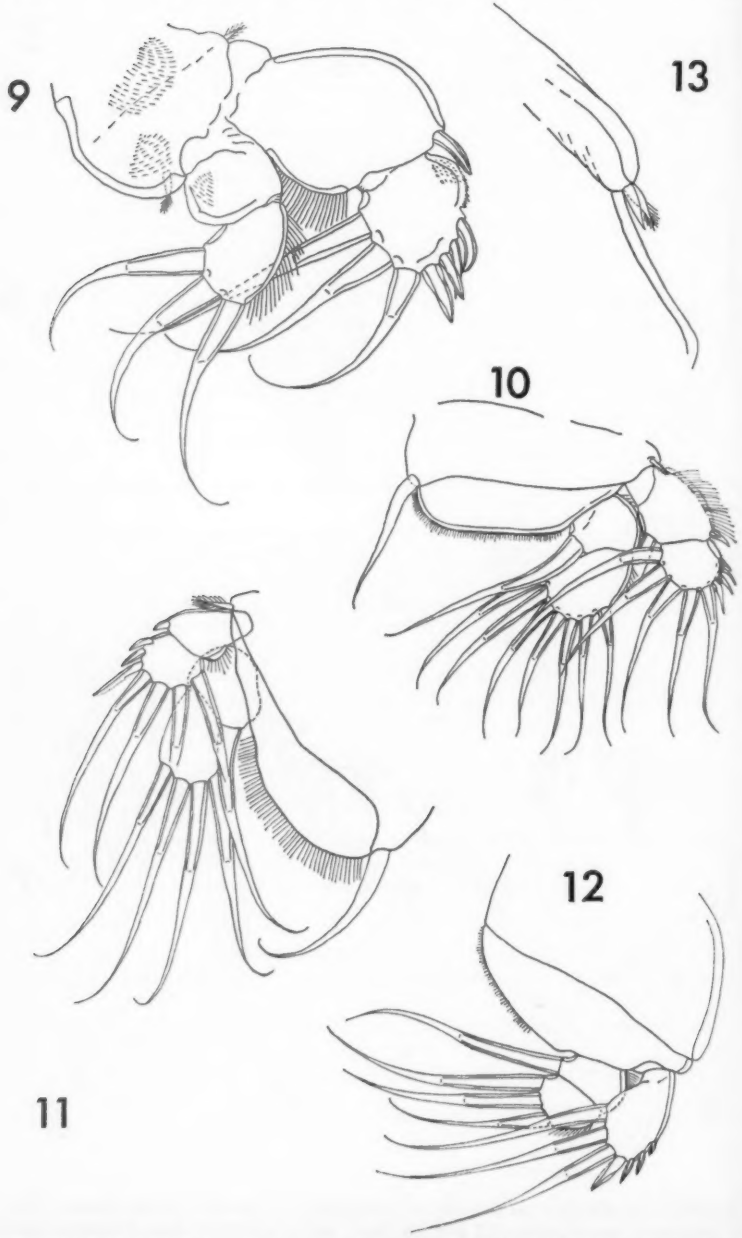
STOSSICH, M.
1880. Prospetto della fauna del mare Adriatico, 3: Classe V, Crustacea. Bull. Soc. Adriatica Sci. Nat. Trieste, vol. 5, no. 5, pp. 178–271.

VALLE, A. D.
1878. Sopra due specie di crostacei parassiti dell'*Oxyrrhina spallanzani* Raf. Estratto Boll. Sci. Nat., vol. 4, no. 1, pp. 89–92.
1880. Crostacei parassiti dei pesci del mare Adriatico. Boll. Soc. Adriatic Sci. Nat., vol. 6, pp. 55–90.

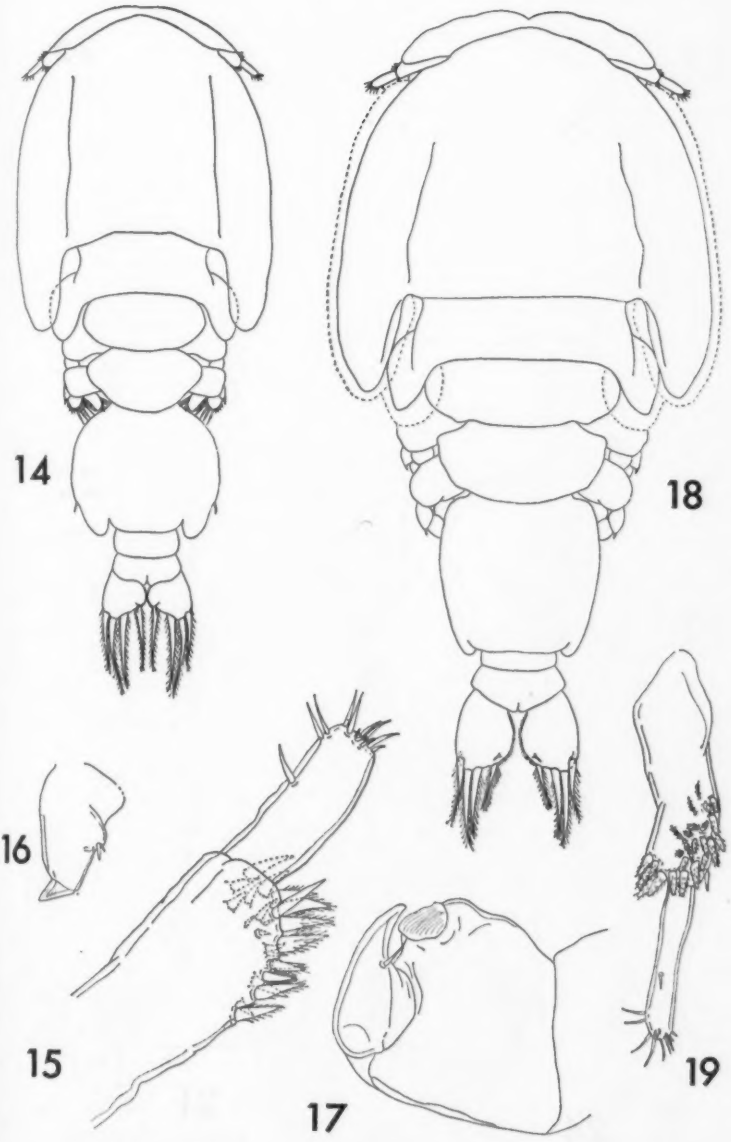
WILSON, C. B.
1922. North American parasitic copepods belonging to the family Dichelesthiidae. Proc. U. S. Nat. Mus., vol. 60, no. 2400, pp. 1–100.
1923. Parasitic copepods in the collection of the Riksmuseum at Stockholm. Ark. Zool., vol. 15, no. 3, pp. 1–15.
1932. The copepods of the Woods Hole region, Massachusetts. U. S. Nat. Mus. Bull. 158, 635 pp.



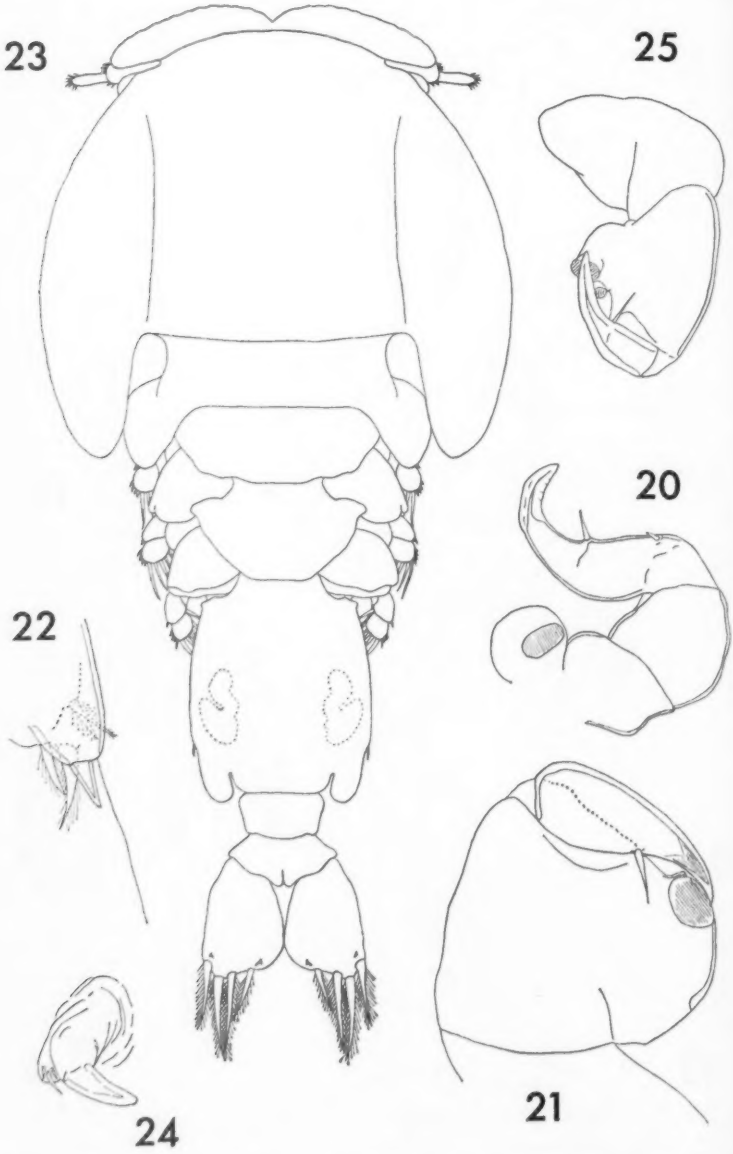
FIGURES 1–8.—*Phyllothereus cornutus*, male copepodid: 1, dorsal; 2, caudal ramus; 3, first antenna; 4, second antenna; 5, first maxilla; 6, second maxilla; 7, base of terminal claws on second maxilla; 8, maxilliped.



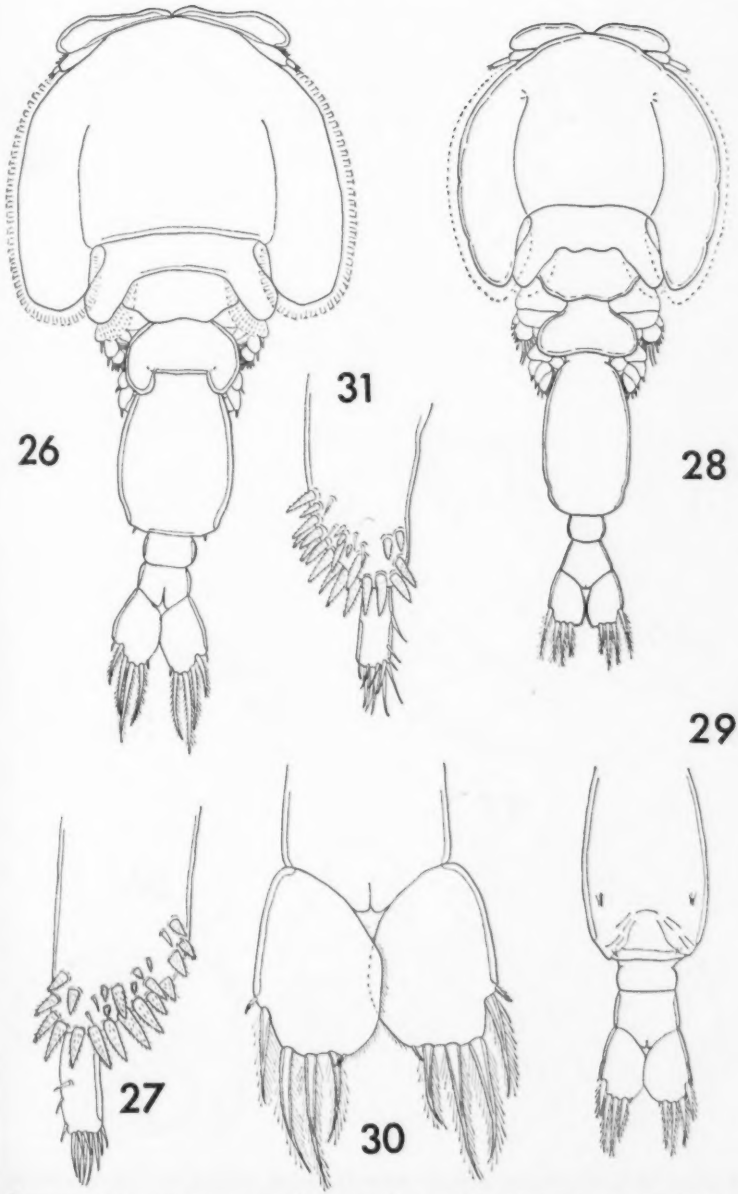
FIGURES 9–13.—*Phyllothereus cornutus*, male copepodid: 9, leg 1; 10, leg 2; 11, leg 3; 12, leg 4; 13, leg 5.



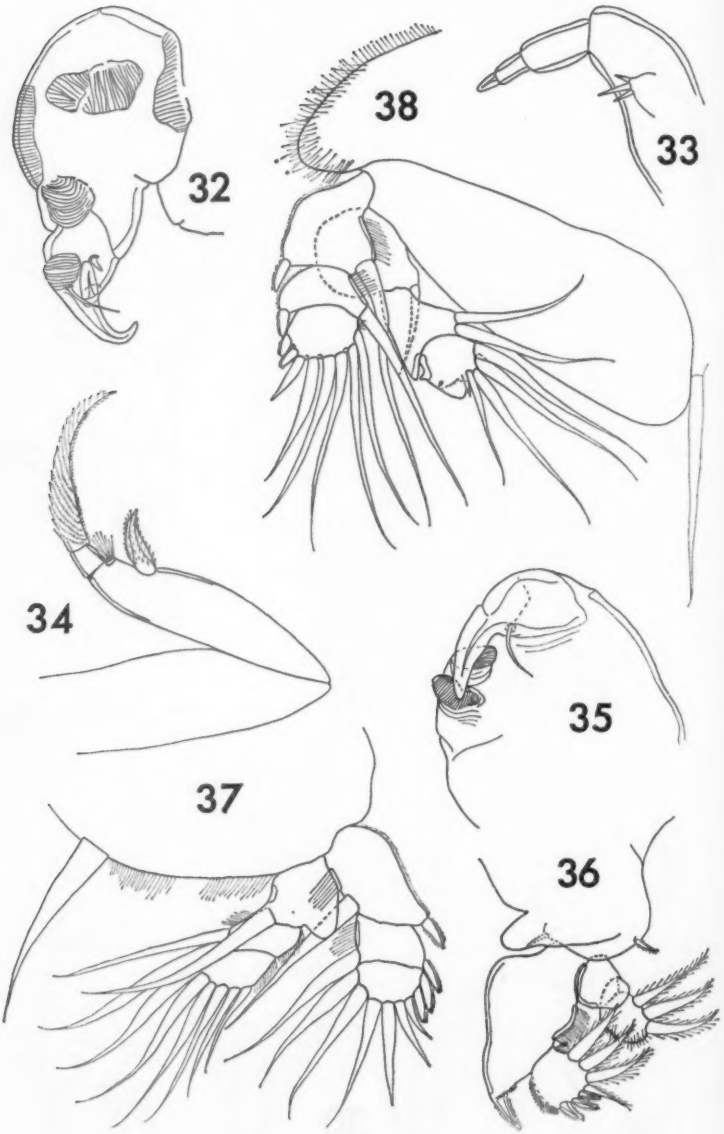
FIGURES 14–19.—*Phyllothereus cornutus*, male chalimus I: 14, dorsal; 15, first antenna; 16, first maxilla; 17, maxilliped. Male chalimus II: 18, dorsal; 19, first antenna.



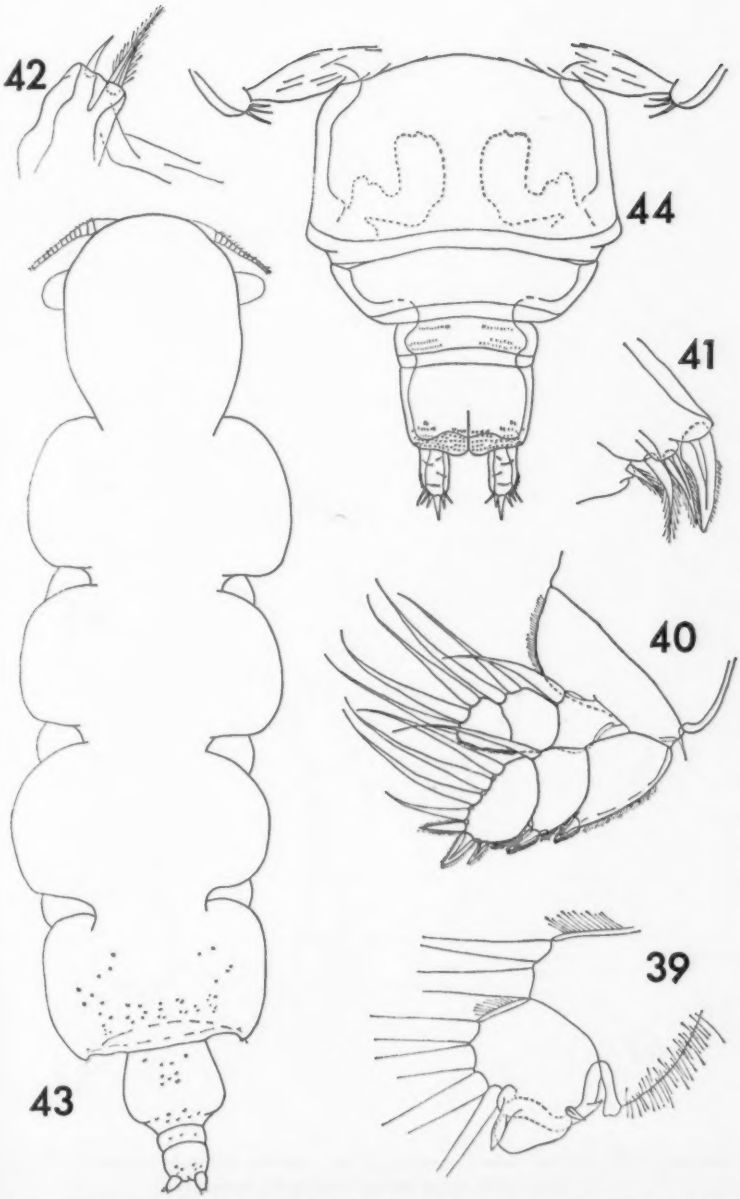
FIGURES 20–25.—*Phyllothereus cornutus*, male chalimus II: 20, second antenna; 21, maxilliped; 22, leg 5. Male chalimus III: 23, dorsal; 24, first maxilla; 25, maxilliped.



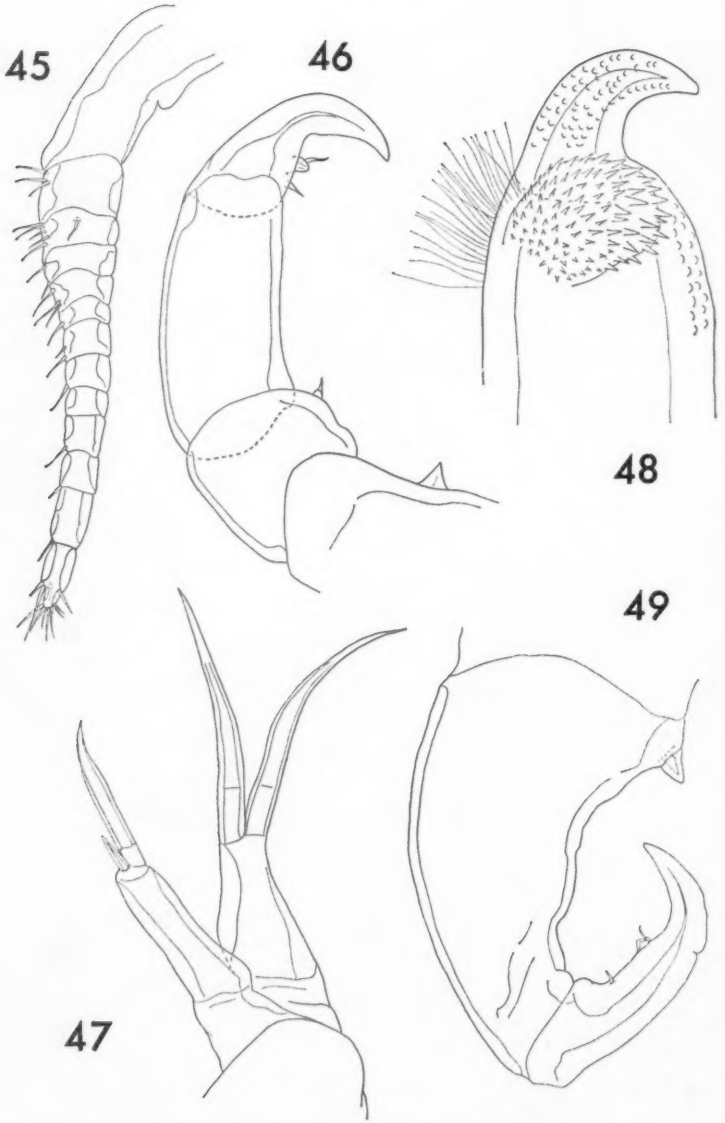
FIGURES 26–31.—*Dinemoura latifolia*, male: 26, dorsal; 27, first antenna. *D. producta*, male: 28, dorsal; 29, genital segment and abdomen, ventral; 30, caudal rami; 31, first antenna.



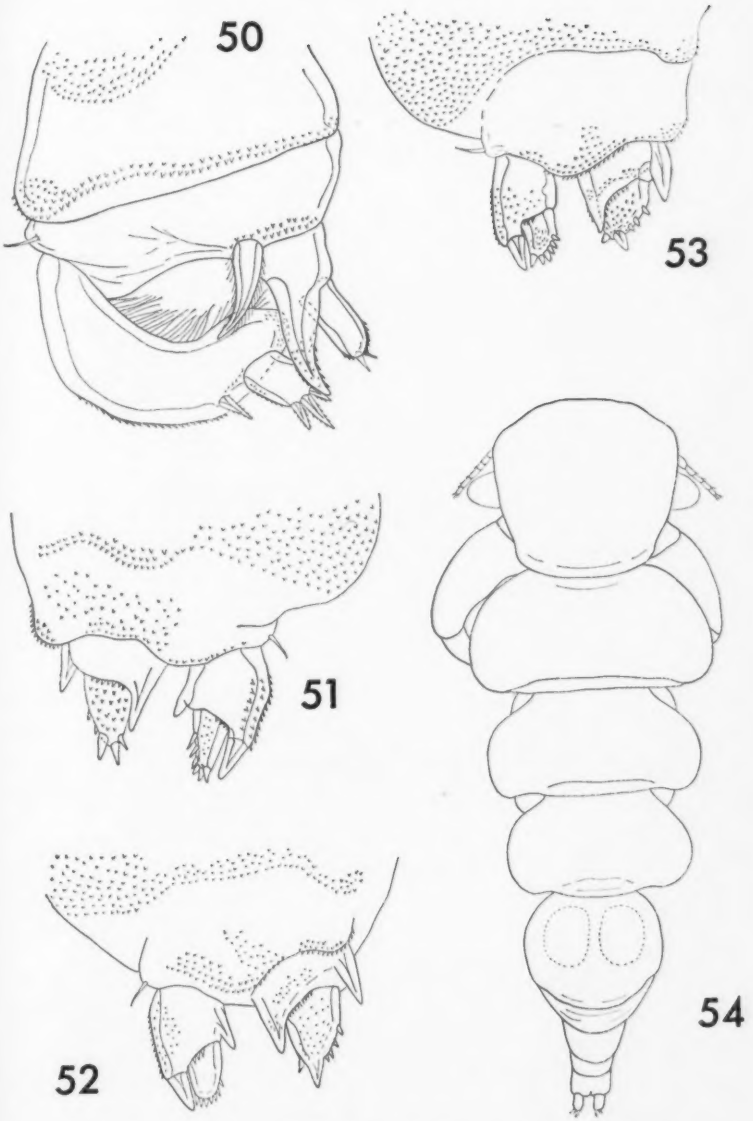
FIGURES 32–38.—*Dinemoura producta*, male: 32, second antenna; 33, first maxilla; 34, second maxilla; 35, maxilliped; 36, leg 1; 37, leg 2; 38, leg 3.



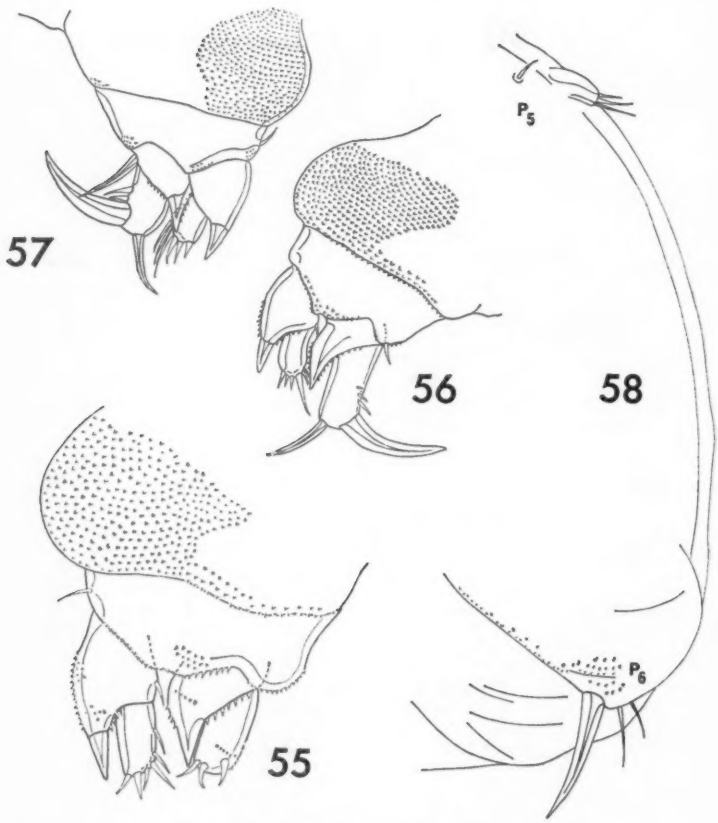
FIGURES 39–44.—*Dinemoura producta*, male: 39, terminal segment on endopod of leg 3; 40, leg 4; 41, leg 5; 42, leg 6. *Nemesis lamna*, female: 43, dorsal; 44, genital segment and abdomen, ventral.



FIGURES 45–49.—*Nemesis lamna*, female: 45, first antenna; 46, second antenna; 47, first maxilla; 48, tip of second maxilla; 49, maxilliped.



FIGURES 50–54.—*Nemesis lamna*, female: 50, leg 1; 51, leg 2; 52, leg 3; 53, leg 4. Male: 54, dorsal.



FIGURES 55–58.—*Nemesis lamna*, male: 55, leg 2; 56, leg 3; 57, leg 4; 58, edge of genital segment showing legs 5 and 6.

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